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1 **Article type: Research Article**

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3 **Oribatid mites show how climate and latitudinal gradients in organic matter can drive**
4 **large-scale biodiversity patterns of soil communities**

5

6 **Short running title:** *Macroecological determinants of soil animals*

7

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28 coordinating and conducting the 1998 Countryside Survey and subsequent processing of
29 samples. We thank three anonymous reviewers for their constructive comments.

30

31 **Abstract**

32 Aim: The factors determining spatial distributions and diversity of terrestrial invertebrates are
33 typically investigated at small scales. Large-scale studies are particularly missing for soil
34 animals, which control microbial communities and represent one of the most diverse yet
35 poorly known animal assemblages. Here, we analyzed a major group (Oribatida) to test
36 whether belowground macroecological patterns can be predicted by climatic variables,
37 vegetation, and large-scale variation in key soil properties.

38 Location: we modelled the multivariate distribution of more than 100 species using
39 biodiversity data collected across Great Britain in the framework of the Countryside Survey
40 (<http://www.countrysidesurvey.org.uk>).

41 Methods: We analysed species-level data from 582 samples collected across 162 hectads
42 (10 × 10 km) covering the largest possible range of vegetation types, soil properties and
43 climatic conditions within GB. We created the first large-scale maps of soil animal diversity
44 metrics at the GB scale, including novel estimates of metrics of phylogenetic diversity. Using
45 structural equation modelling, we quantified the direct and indirect effects of location
46 (latitude, longitude), plant community structure, and abiotic factors such as precipitation on
47 species composition, richness, and phylogenetic diversity.

48 Results: We found that variation in species composition follows a latitudinal gradient with
49 diversity generally increasing northward. The latitudinal variation in species composition
50 drives phylogenetic diversity via changes in both species richness and phylogenetic distance
51 between species. This gradient is mostly determined by latitudinal variation in precipitation
52 and organic matter, which were very good predictor of species composition. Precipitation
53 and organic matter were, however, relatively weak while statistically significant predictors of
54 diversity metrics.

55 Conclusions: Past studies have emphasized the unpredictability of species distributions and
56 variation in species composition in hyper diverse soil animal communities. However, past
57 studies were conducted at small scales, where stochastic factors may weaken the signal of
58 deterministic factors. Oribatid mites in our study show for the first time that large scale
59 latitudinal gradients in climate and organic matter predict not only variation in species
60 composition but also taxonomic and phylogenetic diversity of soil animal communities.

61 **Keywords:** soil macroecology; animals; diversity; distribution; community phylogenetics;
62 Oribatida

63 **1. Introduction**

64 In the last two decades, one of the major goals of ecology has been to understand the
65 relative roles of the many factors that structure ecological communities in space and time but
66 the majority of studies have focused on aboveground communities, particularly plant
67 communities (Chesson, 2000; Clark & McLachlan, 2003; Hubbell, 2005; Levine &
68 HilleRisLambers, 2009). More recently, ecologists have started to better investigate the
69 interactions between aboveground and belowground communities and how these
70 interactions drive the composition and diversity of both communities (Kardol et al., 2006; Van
71 Der Heijden et al., 2008; de Vries et al., 2012; Prober et al., 2015). Traditionally, most
72 studies investigating aboveground-belowground linkages have been conducted at relatively
73 local spatial scales but some regional and global scale analyses of soil microbial
74 communities have shed light on the large scales determinants of these communities (Fierer
75 et al., 2009; de Vries et al., 2012; Ramirez et al., 2014). Local and fine scale variation seems
76 mostly due to interactions determined by the patchy distribution of resources and plant
77 species (Bezemer et al., 2010; Thomson et al., 2010) while spatial gradients in vegetation
78 types and abiotic factors such as pH and climatic conditions are the major correlates of
79 microbial distribution at regional scales (Fierer et al., 2009; Griffiths et al., 2011). Protists,
80 too, follow similar macroecological patterns (Soininen, 2011). For some groups such as
81 arbuscular mycorrhizal fungi (AMF), global studies have started to reveal the relative roles of
82 local, regional and historical factors on community structure and diversity (Davison et al.,
83 2015) but for soil animals large-scale studies are missing despite some synthesis data
84 having provided insight in the macroecology of soil arthropods, nematodes and oligochaetes
85 (Decaëns, 2010; Brusaard et al., 2012; Nielsen, 2014). Studies focusing on selected
86 assemblages at relatively local scales (Lindo & Winchester, 2009; Nielsen et al., 2010;
87 Caruso et al., 2011) have shown that, similarly to microbial communities, soil animal
88 communities are structured at multiple spatial scales, with many species being dispersal-
89 limited over certain scales (Ettema & Wardle, 2002; Wardle, 2006) and soil environmental

90 heterogeneity being high already at very small scale (e.g. <100cm; Ettema & Wardle 2002).
91 This small scale heterogeneity promotes community diversity in both animals and microbes
92 and is mostly due to small scale variation in soil properties such as pH, the concentration of
93 organic matter and key nutrient such as P and N, and also structural variation in soil such as
94 variation in the physical distribution of aggregates (Dumbrell et al., 2010; Nielsen et al.,
95 2010). Nevertheless, much spatial variation in the structure and diversity of soil communities,
96 especially animals, is often left unexplained by variation in environmental variables or other
97 biotic factors. Previous studies have hypothesised that stochastic population dynamics,
98 including dispersal limitation, may sometimes play a major role in this variation (Lindo &
99 Winchester, 2009; Caruso et al., 2011). At large scales, the few studies available on soil
100 animals have concentrated on classical macroecological patterns such as species-area
101 relationships, altitudinal and latitudinal gradients in diversity and some insight on patterns of
102 phylogenetic diversity (see review in Brusaard et al., 2012) but most datasets focused on the
103 highest taxonomic ranks (e.g., family or class level; Nielsen, 2014) or, as noted by Decaëns,
104 (2010) are biased in terms of sampling efforts towards temperate countries, and in general
105 lack the resolution necessary to disentangle the contribution of multiple factors at multiple
106 spatial scales. The only quantitative study on the regional variation of soil animal
107 communities at the species level (Zaitsev *et al.* 2013) showed that studies conducted at
108 relatively small scales cannot capture the long-term effects of the historical processes that
109 contribute to large scale gradients in species richness and community composition. Overall,
110 large-scale studies that help disentangle the roles of abiotic and biotic factors that structure
111 soil communities at regional scales are in their infancy.

112 Here we focused on a unique dataset of the species of oribatid mites collected during the
113 first assessment of soil biodiversity across Great Britain undertaken in 1998 (known as the
114 GB Countryside Survey or CS: <http://www.countrysidesurvey.org.uk>). This survey produced
115 a baseline dataset across all major soil types and habitats (Black et al., 2002) and showed
116 that populations of microbes and microarthropods varied across major environmental zones,

117 vegetation classes and soil types (Black et al., 2003; Griffiths et al., 2011; Keith et al., 2015).
118 Oribatid mites (Acari, Acariformes) are a cornerstone of soil food webs worldwide: over
119 10,000 species have been described and they can reach densities of up to 400,000 ind./m²
120 in forest soils, although they occur in all biomes including continental Antarctica (Coleman et
121 al., 2004). Oribatid mites are one of the most ancient groups of terrestrial animals and have
122 been part of the soil food webs ever since soil have appeared on the geological record about
123 400 mya (Shear et al., 1984; Norton et al., 1988). They appear for the first time in the fossil
124 record of the Devonian site of Rhynie Chert (407-397 mya, Aberdeenshire, Scotland)
125 although a relatively recent molecular clock suggests a much earlier origin (Schaefer et al.,
126 2010). For all these reasons, oribatid mites provide an excellent model to analyze the role of
127 abiotic and biotic factors in structuring diversity and composition of belowground animals at
128 regional scales. We used the dataset of oribatid mites to conduct a species-level analysis of
129 the determinants of community structure and diversity of this major group of soil animals.
130 The CS is a unique audit of vegetation, soils, habitats and landscape across GB that began
131 in 1978 (Firbank et al., 2003; Keith *et al.* 2015). Using a spatially explicit approach, we
132 created the first maps of diversity metrics at the GB scale for a major soil animal group,
133 including the first estimates of phylogenetic diversity (Faith, 1992; Cadotte et al., 2010) and
134 used structural equation modelling (Grace, 2006) to estimate the direct and indirect effects of
135 location (latitude, longitude), abiotic factors such as precipitation, and plant community
136 structure on oribatid mite species composition and diversity. We hypothesized that large-
137 scale gradients in this belowground community are directly driven by large-scale gradients in
138 abiotic factors (e.g., climatic variables) but also via the effects of these factors on plant
139 community structure and edaphic properties such as organic matter.

140

141

142

143 **Methods**

144 *Database Background*

145 The data analysed in this study were collected in the framework of the Country Survey audit
146 (Firbank et al., 2003; Keith *et al.* 2015). This environmental audit is based on a stratification
147 of GB into land classes, each land class being characterised by a combination of climate,
148 altitude and location (Firbank et al., 2003; Sheail & Bunce, 2003). Each sampling location
149 was assigned a Broad Habitat (BH) and an Aggregate Vegetation Class (AVC). BH is a
150 classification consisting of 27 habitats that are used in the Land Cover Map accounting for
151 the entire land surface of GB, and AVC is a high-level grouping of vegetation types produced
152 from a classification of plant communities from the original CS vegetation plots and includes
153 eight categories (crops and weeds, tall grass and herb, fertile grassland, infertile grassland,
154 lowland woodland, upland woodland, moorland-grass mosaic, and, heath and bog (Bunce et
155 al., 1999). Specifically, we analysed 582 samples mostly collected between 29 May and 28
156 October in 1998 with some samples collected between June and August in 1999. The
157 samples analysed in this study were collected across 162 10 x 10 km plots (hectads), with
158 an average of 4 locations sampled within each hectad. Each sample location was associated
159 with information on vegetation, soil properties and land-use, produced during CS. For the
160 collection of each soil sample, surface vegetation was removed leaving the litter layer intact
161 and a soil core (4 cm diameter, 8 cm depth) was taken. Cores were placed immediately in
162 cool boxes and sent to the laboratory at the Centre for Ecology & Hydrology Lancaster for
163 extraction of invertebrates.

164

165 *2.2 Oribatid extraction and identification*

166 Cores were processed over five days using a dry Tullgren extraction method and all
167 invertebrate specimens collected into 70% ethanol preservative (Emmett et al., 2010) . Once
168 collected, the soil invertebrates were identified to broad taxa, separated and counted under a

169 stereomicroscope. Specimens of Acari (mites) from each extract were removed into another
170 vial and sent for separation and identification of oribatid mites species. Specimens were
171 identified at $\times 400$ magnification and, where necessary, were cleared for 24h using lactic acid
172 at room temperature before being mounted in glass cavity slides. The unpublished
173 monograph of British oribatid mites by M. Luxton and other specialist primary literature were
174 used to identify oribatid mites to the species level; identifications have since been checked
175 against Weigmann, (2006). Weigmann (2006) plus several other specialist publications were
176 also used to define geographic distributions and ecological traits of the taxa. Oribatid species
177 records and taxonomic details were then collated into a dataset that is available upon
178 request from the NERC Environmental Information Centre (see Keith et al. 2018 for details
179 to access the data).

180

181 *2.3 Associated environmental data*

182 Existing soil, vegetation and habitat data from CS were collated for the 582 samples of soil
183 fauna and are available upon request from the NERC Environmental Information Centre (see
184 Barr et al. 2014 and Black et al. 2016 for details to access the vegetation and habitat data)..
185 Soil properties were collected from a separate core taken adjacent to the core used to
186 extract soil animals; soil data included moisture content, pH, organic matter (loss-on-
187 ignition), total C content and total N content. The sampling protocol and detailed methods
188 used for these soil analyses can be found in Emmett et al. (2008) and the data are reported
189 in more detail elsewhere (Reynolds et al., 2013). For vegetation composition, ordination
190 scores were used from the first three axes of a Detrended Correspondence Analysis (DCA)
191 using binary plant species data from the same plots.

192 Climate data associated with each sampling plot was derived from the UKCP09: Met Office
193 gridded land surface climate observations at 5×5 km resolution (Met Office, 2017). These

194 data were used to calculate average values of mean annual temperature and mean annual
195 rainfall for the period 1992–1997, in order to incorporate recent climatic trends.

196

197 *2.4 Statistical analyses*

198 *Community and environmental data*

199 Records of oribatid mites across sampling locations were collated at 10km × 10km/hectad
200 resolution for a total of 162 10 x 10 km squares, and the associated environmental data were
201 averaged at this resolution (see Barr et al. 2014, Black et al. 2016 and Keith et al. 2018 to
202 access the data from NERC Environmental Information Centre).

203 We used the spatial interpolation method of kriging (Matheron, 1963; Wagner, 2003) to
204 illustrate spatial variation in community structure and metric of diversity (see below for the
205 metrics used). The spatial structure of the variables was quantified with the empirical
206 semivariogram (Wagner, 2003; Bivand et al., 2008) and then fitted with a theoretical
207 variogram model (i.e., exponential or Gaussian, or spherical models) to estimate values at
208 unmeasured locations. We used the R library “geoR”, “maps”, “mapdata” and “gstat” for
209 variograms, kriging estimation and mapping of results. See also Bivand et al. (2008) for
210 further details.

211 We used a multivariate regression approach based on Principal Coordinate Analysis
212 (Legendre & Legendre, 1998; Borcard et al., 2004) to quantify the relative importance of
213 location (space) and environment (temperature, plant community composition, pH,
214 precipitation, organic matter) on oribatid mite community structure. PCoA was applied to the
215 Jaccard distance matrix obtained by the presence-absence distribution of species, and a
216 distance based RDA (db-RDA) was used to estimate the effect of space and environment on
217 the multivariate distribution of species.

218 To quantify the effect of “space” (i.e., location), we used latitude, longitude and the method
219 of principal coordinate analysis of neighbour matrices (PCNM; Borcard & Legendre, 2002),
220 which defines a set of spatial factors that parsimoniously account for patterns in species
221 distribution at multiple scales. The final set of PCNM vectors was defined using a
222 multivariate extension of the Akaike information criterion (AIC; Dray et al., 2006). Variance
223 partitioning was computed to estimate the amount of fraction uniquely attributable to space
224 and environment, and the variation shared between space and environment (Borcard et al.,
225 1992; Legendre & Legendre, 1998). Besides observed species number per hectad we also
226 calculated species rarefaction curve (Gotelli & Colwell, 2001) for each hectad and estimated
227 the hectad asymptotic richness using the Chao estimator (O’Hara 2005; Chiu *et al.* 2014). All
228 multivariate analyses and estimates of species richness were performed using the R
229 package “vegan” (Oksanen et al., 2007).

230

231 Phylogenetic methods

232 The phylogenetic tree was reconstructed based on 18S rDNA. Sequences were downloaded
233 from NCBI (<https://www.ncbi.nlm.nih.gov>) or, if not available, were newly generated
234 sequenced at the J.F. Blumenbach Institute of Zoology and Anthropology, University of
235 Göttingen.

236 Genomic DNA was extracted from single individuals using the DNeasy® Blood and Tissue
237 Kit (Qiagen, Manchester, UK) following the manufacturer’s protocol for animal tissue.
238 Amplification of the 18S region was performed in 25 µl volumes containing 12.5 µl
239 HotStarTaq Mastermix (Qiagen), 5 µl of template DNA, 1 µl of each primer (100 pM) and 5.5
240 µl H₂O. Primers for PCR were 5’ -TAC- CTGGTTGATCCTGCCAG-3’ (forward) and 5’ -
241 TAATGATCCTTCCGC AGGTTAC-3’ (reverse) (Domes et al., 2007). The PCR protocol
242 consisted of an initial activation step at 95 °C for 15 min, 35 amplification cycles (95°C for 45
243 s, 57° C for 60 s, 72°C for 60 s) and a final elongation step at 72 °C for 10 min. All PCR

244 products were visualized on a 1% agarose gel, purified with the QIAquick PCR Purification
245 Kit (Qiagen), and sequenced by Microsynth Seqlab (Göttingen, Germany), using the
246 additional sequencing primers 18S554f 5'-AAGTCTGG TGCCAGCAGCCGC-3' , 18S1282r
247 5'-TCACTCCACCAACTA AGAACGG C-3' , 18S1150f 5' -
248 ATTGACGGAAGGGCACCACCAG-3' and 18S614r 5'- TCCAACACTACGAGCTTTTTTAACC-3'
249 (Domes et al., 2007). In total, we used 51 species for the phylogenetic tree, including four
250 outgroup taxa. All taxa and accession numbers are available at GenBank (Supporting
251 Information, Appendix S1, Table S1). We aimed to represent each family in the GB dataset
252 with at least one species but very few rarer species could not be represented either because
253 sequences are not available in public database or because we did not have sufficient
254 material to sequence them. In total, the dataset represents 31 out of the 34 families found in
255 the GB dataset and the three families we could not represent were very rare and present
256 with very low abundances. Sequences were assembled and ambiguous positions were
257 corrected in Sequencher 5.3 (Gene Codes Corporation, Ann Arbor, Michigan, USA) and
258 aligned using ClustalW implemented in BioEdit v7.0.1 (Hall, 1999) with the multiple
259 alignment parameters gap opening = 30 and gap extension = 0.3.

260 The alignment was truncated to the shortest sequence resulting in a length of 1,743 bp
261 including gaps. Evolutionary model parameters were determined with jModelTest v2.0
262 (Guindon & Gascuel, 2003; Darriba et al., 2012) using the AIC. The best-fit model for
263 sequence evolution for 18S was GTR + I + G. The phylogenetic tree was constructed in R
264 using packages “ape” and “phangorn” (Paradis et al., 2004; Schliep 2011, Schliep et al.,
265 2017) using Maximum Likelihood and 1,000 bootstrap replicates. The phylogenetic tree was
266 reduced to 31 oribatid mite taxa representing one species per family using the drop.tip
267 function, the R script is provided in the Appendix S1 (Supporting Information)

268 We used this oribatid mite phylogenetic tree to calculate metrics of phylogenetic diversity.
269 The resolution of the available phylogenetic information constrained us to calculate these
270 metrics at the family level. Specifically, we calculated the Faith's Index PD (Faith, 1992) and

271 two distance based metrics: the mean phylogenetic distance (MPD) and the mean nearest
272 taxon distance (MNTD). The index PD estimates the phylogenetic diversity of a community
273 as the sum of the tree branch lengths connecting all species in the assemblage and as such
274 it can be considered an estimate of point diversity with two components: species richness
275 and amount of phylogenetic information across all the species in the assemblage. The
276 indices MPD and MNTD measure the average phylogenetic distance between species in an
277 assemblage. The MPD is based on mean distance of any taxon from every other taxon while
278 MNTD is average of the distance between any taxon and its closest relative. Community
279 phylogenetic metrics were calculated using the R package “picante” and other packages that
280 support phylogenetically informed statistical analyses (“ape”,
281 “phylobase”, “adephylo”, “phytools”; Swenson, 2014)

282

283 *Structural equation modelling (SEM)*

284 In order to quantify direct and indirect effects of climatic and soil variables (temperature,
285 plant communities, pH, precipitation, organic matter) on community species composition
286 (PCoA ordination axes) and diversity (richness and metric of phylogenetic diversity) we used
287 Structural Equation Modelling (Grace, 2006). We started from an *a priori* model (Appendix
288 S2, Fig. S1 in the Supporting Information) assuming that latitude, longitude and elevation
289 drive the spatial variation of climate (i.e. precipitation and temperature), which correlates with
290 spatial variation in organic matter. The variation in climate and organic matter then drives
291 spatial variation in oribatid mite species composition. However, other factors that may vary
292 with latitude and longitude, including biogeographical factors, may drive the spatial
293 distribution of oribatid species. Biogeographical factors, which are implicitly accounted for by
294 latitude and longitude, include the major spatially structured features of the geology of Britain
295 (Toghil, 2005), with northern areas (e.g, Scottish highlands) being generally older but also
296 more affected by last glacial maxima than southern areas (e.g., southeast England).

297 Eventually, all these environmental and geological changes in space determined spatial
298 variation both in species composition and metrics of diversity, including species richness and
299 phylogenetic diversity metrics that combined both richness and compositional information.
300 Starting from this conceptual model, we fitted various versions of the model to the data until
301 we obtained a parsimonious model that could adequately fit the data. Model fit was
302 evaluated using the Chi-square test, and the RMSEA and CFI index, while amount of
303 explained variation in community metrics and diversity indices (R-square) was used to
304 measure the predictive power of the model (Grace, 2006; Shipley, 2016). SEM was
305 performed using the R package lavaan (Rosseel, 2011).

306

307 **Results**

308 A total of 141 species were found in this study, which represented more than one third of
309 known oribatid mites in the British Isles (Luxton, 1996) and the vast majority of belowground
310 species (the CS survey specifically focused on soil species while oribatid mites also live on
311 aboveground moss and tree canopy). Observed species richness ranged from 1 to 28 while
312 the Chao's estimator ranged from 1 to 161 species. Hectads with very low species richness
313 always included arable and very infertile grassland soil, where environmental conditions
314 typically supported only very poor oribatid mite communities or no oribatids at all. These
315 soils were colonised only by very few opportunistic species such as some of the species in
316 the genera *Tectocepheus*, *Liochthonius* and *Pantelozetes*. On the contrary, hectads with
317 high species richness tended to be characterised by woodland or organic soils, where
318 oribatid mites are known to be abundant. Observed hectad species richness displayed both
319 clear latitudinal and longitudinal gradients with hectads in north-west Scotland being richer
320 than in south-east England (Fig. 1). Instead, Chao's estimator showed a very patchy
321 distribution suggesting the existence of hotspots of species richness, mostly located in
322 central and northern England, and Scotland (Fig. 1).

323 The species-area relationship was best fitted by a sigmoidal model (Fig. 2) meaning the
324 existence of an upper limit below which species richness is relatively, but not completely,
325 independent of area. Also, as area increases species richness is predicted to reach an upper
326 asymptotic level (Lomolino, 2000). The classical power model and semi-log model provided
327 a much poorer fit to the data.

328 The variation in oribatid mite species composition was mostly driven by the covariation
329 between organic matter (LOI), pH, and precipitation and variation in plant species
330 composition, which was almost collinear with amount of organic matter. Although both
331 community structure and environmental variables follow clear latitudinal patterns (Fig. 3), the
332 total amount of variance accounted for by measured environmental variables was only 8%.
333 Yet, this fraction of variation was statistically significant at $P < 0.05$. There was also 6% of
334 variance accounted for by the spatially structured effect of environmental and plant
335 variables. The pure effect of latitude, longitude and PCNMs (i.e., after removing
336 environment) accounted only for 1% of community variance, meaning that the observed
337 spatial variation in the assemblage is mostly co-varying with the spatial structure observed in
338 the environmental variables (6%).

339 Metrics of phylogenetic diversity showed different types of spatial patterns (Fig. 4). The
340 Faith's index showed gradients that were highly correlated to the same ones observed for
341 plot species richness (compare Fig. 4 with Fig. 1) while MPD and MNTD mostly reflected
342 longitudinal gradients. MPD is higher in the North and the East while MNTD seems more
343 variable and reaching the highest value in the South-East (Fig. 4).

344 Structural equation modelling indicated that models including just latitude as a descriptor of
345 position generally outperformed models with both latitude and longitude in terms of global fit
346 metrics. For example, all models with both latitude and longitude resulted in Chi-square with
347 p-values much lower than 0.05 (i.e., model rejected) and with very poor CFI (< 0.9) and
348 RMSEA (> 0.2) values. We therefore retained latitude and removed longitude from the
349 subsequent models. Although latitude could affect indices of diversity both directly and

350 indirectly, models with a direct link between latitude and diversity indices returned very poor
351 global fit metrics and were therefore not considered further. Details on the models
352 considered during the SEM exercise and their performances are provided Appendix S2. The
353 optimal model (Fig. 5) suggests that organic matter is the major driver of oribatid mite
354 community composition and that variation in species composition determines metrics of
355 phylogenetic diversity. Specifically, greater shifts in oribatid mite community assemblages
356 towards that typical of heath, bog and highly organic soil, were associated with higher
357 phylogenetics diversity (positive correlation between PCoA1 and PD) but also lower mean
358 nearest taxon distance (negative correlation between PCoA1 and MNTD). However, there is
359 also an indirect positive effect of PCoA1 on MNTD via PD (positive correlation between PD
360 and MNTD). The model could account for 50, 16 and 5 % of variance in PCoA 1 (major
361 changes in species composition), PD and MNTD, respectively. The full lavaan ouput of the
362 SEM is in Appendix S2 (Supporting Information)

363

364 4. Discussion

365 Soil animal assemblages tend to be very species rich even at small scales. This has been
366 explained as an effect of the high environmental and microbiological heterogeneity that
367 some soil can display already from the 10 m to the sub-metre scale (Anderson, 1975; Giller,
368 1996; Ettema & Wardle, 2002; Nielsen et al., 2010). A surprisingly large fraction of the
369 variation observed in the distribution of soil species is very often left unexplained by variation
370 in key soil variables such as pH and organic C, or even pollutants (Maraun & Scheu, 2000;
371 Caruso et al., 2011, 2017; Maaß et al., 2015). Also, high degrees of stochasticity seem to
372 characterise assembly dynamics of soil animals such as oribatid mites and collembolans at
373 least at small to medium scales (Maaß et al., 2014; Dirilgen et al., 2018). Still, species
374 distributions seem structured at small and medium scales even when spatial structure
375 cannot be explained by spatial gradients in environmental variables (Caruso et al., 2011;
376 Zaitsev et al., 2013). At the regional scale of the Netherlands, Zaitsev *et al.* (2013) found that

377 oribatid mite communities significantly changed along the East-West direction in the absence
378 of a significant variation in precipitation and mean annual temperature. However, geological
379 age (bedrock) and amount and quality of organic matter did change from East to West
380 supporting richer communities in the older forest sites (Zaitsev *et al.* 2013). Our dataset
381 supports this idea at the much broader scale of Great Britain, which is characterised by a
382 relationship between climatic gradients and organic matter: in Britain very organic rich soils
383 (i.e. bogs and peatlands) are mostly found in the North and West, and are characterised by a
384 colder winter climate with more precipitation. Thus, as mean annual precipitation increases
385 with latitude so does organic matter. This is reflected in our data by statistically significant,
386 latitudinal changes in the oribatid mite communities, which prefer organic soil and woodland
387 over low fertile grassland and cropland. Land use could also contribute to these patterns
388 because, in GB, land is generally much more exploited for intensive farming in the south
389 (e.g., England) than the north (Highlands in Scotland). However, our analysis independently
390 accounted for vegetation types and latitudinal gradients in other properties and our results
391 suggest a prominent role of organic matter *per se*. That means that, given the same land use
392 and vegetation type, sites with higher organic matter are associated to specific oribatid mite
393 composition and higher diversity overall. Species richness and metrics of phylogenetic
394 diversities, too, follow this latitudinal gradient in community structure although metrics of
395 phylogenetic diversity that take into account phylogenetic distance between species (MPD
396 and MNTD) show patterns more complex than just a latitudinal gradient. The SEM showed
397 that variation in distance based metrics of phylogenetic diversity (e.g., MNTD) seemed
398 mostly explained by latitudinal changes in species composition rather than accumulation of
399 species richness and phylogenetic diversity (PD). In fact, the direct and negative effect of the
400 latitudinal changes in species composition on MNTD was statistically significant while the
401 direct and positive effect of PD on MNTD was not. The negative correlation between the
402 latitudinal gradient in oribatid mite composition and MNTD suggests that the more the
403 oribatid community moves to the species composition typical of woodland and highly organic
404 soils the less the phylogenetic distance is between a species and its closest relatives in the

405 local assemblages. This result suggests a process of environmental filtering and
406 convergence toward specific assemblages (Webb, 2000). The SEM, however could explain
407 only 5% of the variance observed in MNTD and 16% of the variance observed in PD
408 suggesting that the measured environmental variables are generally weak predictors of
409 these broad biodiversity metrics. On the contrary, the SEM could explain about 50% of the
410 variance observed in the latitudinal gradient in species composition, which implies species
411 composition is much more predictable than compound metrics of biodiversity such as
412 phylogenetic diversity (PD). Specifically, the latitudinal changes in species composition seem
413 best explained by latitudinal variation in organic matter and precipitations, regardless of
414 variation in phylogenetic diversity.

415 Latitude directly correlates with precipitation and organic matter distribution merely because
416 of the north-south climatic gradient. When taking into account the direct and indirect effects
417 of latitude, precipitation and organic matter on oribatid mite species composition, the
418 strongest effect was that of organic matter. Precipitation, too, had a statistically significant,
419 direct effect on community structure but the effect was much smaller than that of organic
420 matter, which is consistent with Zaitsev *et al.* (2013). Instead, the direct effect of latitude on
421 species composition was small and not statistically significant, which implies that latitudinal
422 changes in species composition are driven by latitudinal changes in other variables, namely
423 precipitation and organic matter. Alternative SEMs that linked latitude, longitude, organic
424 matter and precipitation directly to metrics of diversity had a very poor global fit supporting
425 the notion that large-scale gradients in soil oribatid mite diversity are driven by the factors
426 that drive changes in species composition. Still, changes in species composition explained
427 only a relatively small fraction of changes in species richness and phylogenetic diversity,
428 suggesting a potential role for smaller scale heterogeneity. This heterogeneity is not
429 captured by our predictors and suggests that microscale variation in edaphic properties
430 remain a fundamental driver of species distribution and diversity in these communities. This
431 is confirmed by the fact that some hectads resulted to be biodiversity hotspot in terms of

432 estimated species richness. We could not resolve the variables driving this patchy pattern
433 but we speculate that this is driven by soil environmental heterogeneity within hectads, which
434 could be caused by unmeasured variation in habitat fragmentation and land-use intensity
435 (see also supplementary results in the Supporting Information, Appendix S3, Table S2)

436 Despite the latitudinal patterns observed in oribatid mites and contrary to what has been
437 observed in small- and medium-scale studies (Caruso et al., 2011; Maaß et al., 2015), the
438 investigated community had limited spatial structure, even when considering spatial variation
439 that is not explainable by spatial structure in environmental variables. In comparison, the
440 microbial communities of GB seem to be much more spatially structured (Griffiths et al.,
441 2011), which suggests the interesting hypothesis of a decoupling between large-scale
442 patterns in soil microbes and animals.

443

444 **Conclusions**

445 Latitudinal gradients in organic matter are the most important predictor of latitudinal changes
446 in species composition of oribatid mites across the spatial extent of Great Britain. These
447 changes partially drive variation in species richness and phylogenetic diversity but a
448 significant fraction of the variation observed in these metrics remained unexplained,
449 suggesting a potential role for unmeasured environmental heterogeneity at medium and
450 small scales. Despite small and medium scale heterogeneity, macroecological patterns in
451 this major group of soil animals are predictable by the climatic factors that control variation in
452 plant community structure and organic matter.

453

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637 spatial trends in oribatid mite diversity. *Landscape Ecology*, **28**, 285–296.
- 638
- 639 **Data accessibility statement:** The data supporting the results are available from the
640 Environmental and Information Data Centre of NERC (UK). The spatial coordinates require a
641 license agreement to be accessed.
- 642

643 **Biosketch**

644 **Tancredi Caruso** is a quantitative ecologist investigating the processes that structure
645 terrestrial biodiversity in space and time

646 **Ina Schaefer** is an evolutionary biologist with expertise on soil fauna

647 **Aidan M Keith** is an ecologist investigating land use and climate impacts on soil biology

648 **Frank Monson** is a soil animal taxonomist

649

650 All authors developed the concept of the paper; AMK and FM compiled and collected the
651 data, TC analysed the data, IS compiled and collected molecular data and constructed the
652 phylogenetic trees. All authors contributed substantially to the writing of the ms

653

654 **Figure Legends**

655 **Figure 1** a) species richness and b) Chao's estimator of species richness for each 10 × 10
656 km plots. The maps were obtained via kriging interpolation at the hectad scale. Red
657 represents high values, yellow low values. Species richness (a) displays a clear latitudinal
658 gradient with richness increasing northward along the southwest-northeast direction whereas
659 Chao's estimator (b) displays a patchy distribution suggesting the existence of hotspots if
660 species richness.

661

662 **Figure 2** Species-area relationships for the oribatid mites of Great Britain. The three fitted
663 models (power law, semi-log, sigmoidal) all fit the data reasonably well but the AIC criterion
664 clearly shows that the sigmoidal model provides the best fit (blue dotted line)

665

666 **Figure 3** PCoA ordination of oribatid mites (a). The first axis is a gradient that follow
667 changes in vegetation, with more organic and woodland soil scoring on the positive side of
668 PCoA1 and grasslands and arable soil on the negative side of PCoA1. This gradient is also
669 correlated to organic matter, latitude, and precipitation, which are all positively correlated
670 with PCoA1. In fact, a kriging interpolation of PCoA1 show a clear latitudinal gradient (b)

671

672 **Figure 4.** Kriging interpolation of three metric of Phylogenetic Diversity. The Faith's index (a)
673 showed gradients that were very correlated to the same ones observed for plot species
674 richness (Fig. 1a) while MPD and MNTD mostly reflected longitudinal gradients although
675 MPD reaches the highest values in the North and the East while MNTD seems more variable
676 and reaching the highest value in the South-East.

677

678 **Figure 5** Structural equation model linking latitude and abiotic parameters to oribatid mite
679 species composition (PCoA1 of Fig. 3) and diversity (Faith Index PD and Mean Nearest
680 Taxon Distance or MNTD of Fig. 4). Species richness was highly correlated to PD and was
681 thus excluded, while MNTD and MPD returned similar results in this SEM and we selected
682 MNTD, which provided the best fit. The model is supported by all metrics of global fit (Chi-
683 square = 8.809 with 9 df and p-value of 0.185, CFI = 0.989 and RMSEA = 0.059). Figures
684 besides the arrows are the path standardised coefficients. Black arrow stands for positive
685 coefficient and gray arrows for negative coefficients. Paths statistically significant at p-value
686 < 0.05 are in bold. All paths were statistically significant except for the direct effect of PD on
687 MNTD and the direct effect of Latitude on PCoA 1. See also Supporting Information b for the
688 full model output, including exact values of path coefficients, R-square values, standard
689 deviations and statistical significance of parameter estimates. The model could account for
690 50, 16 and 5 % of variance in PCoA 1, PD and MNTD respectively. The model could also
691 account for 55 and 17 % of variance in Organic Matter and Precipitation, respectively.

Figure 1

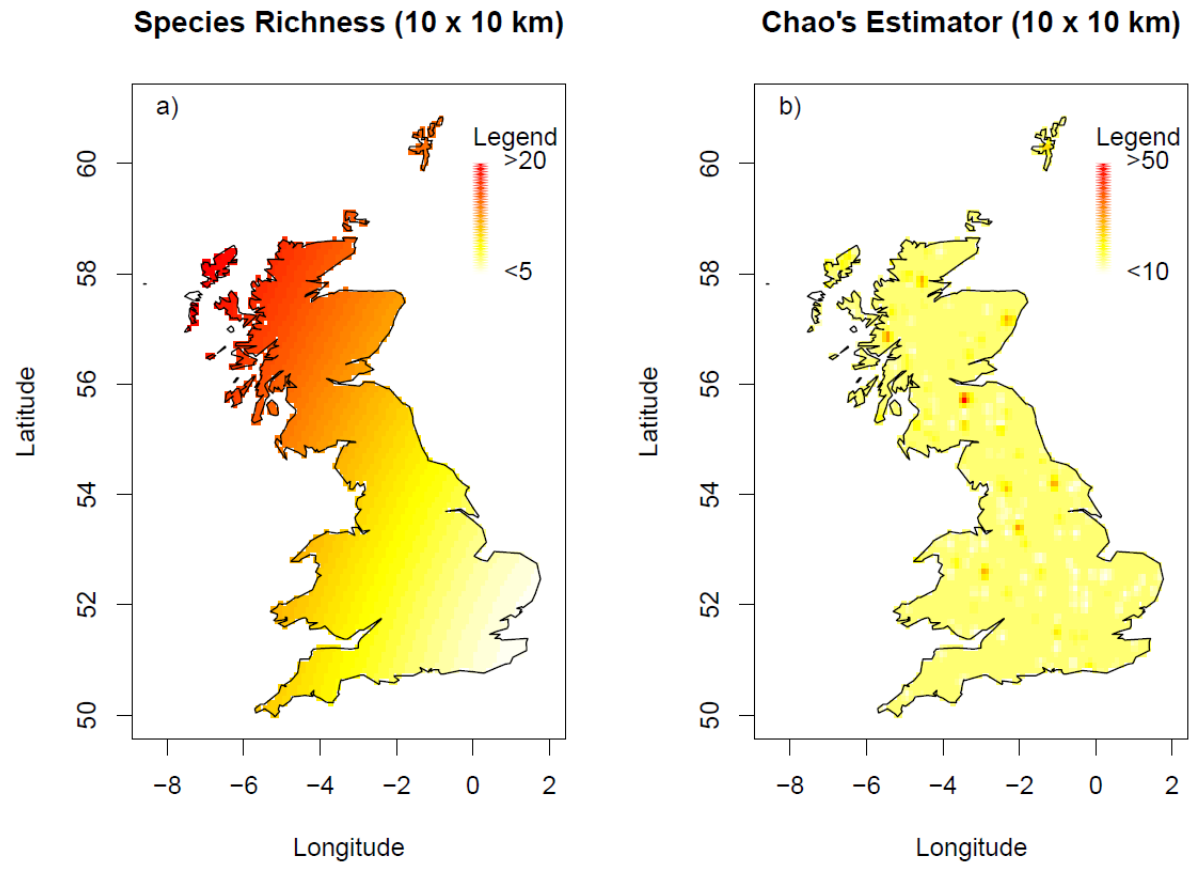


Figure 2

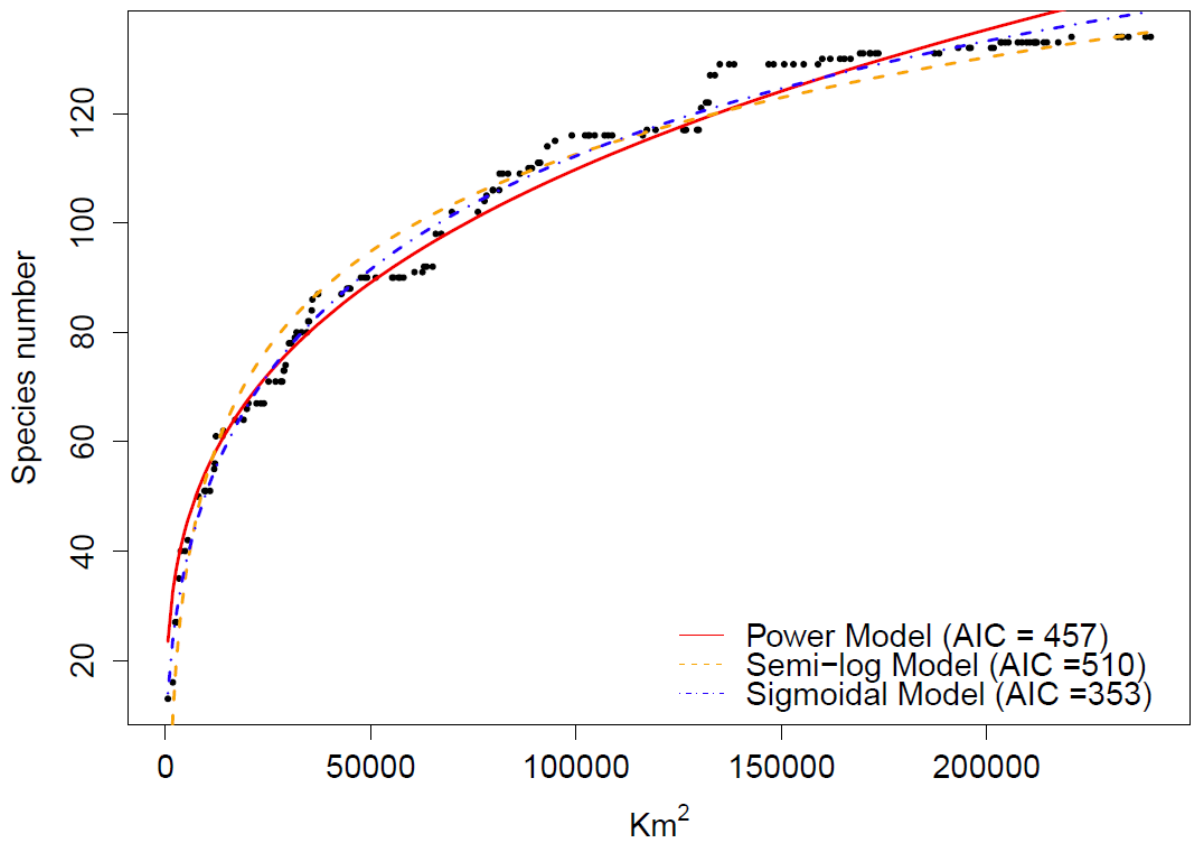


Figure 3

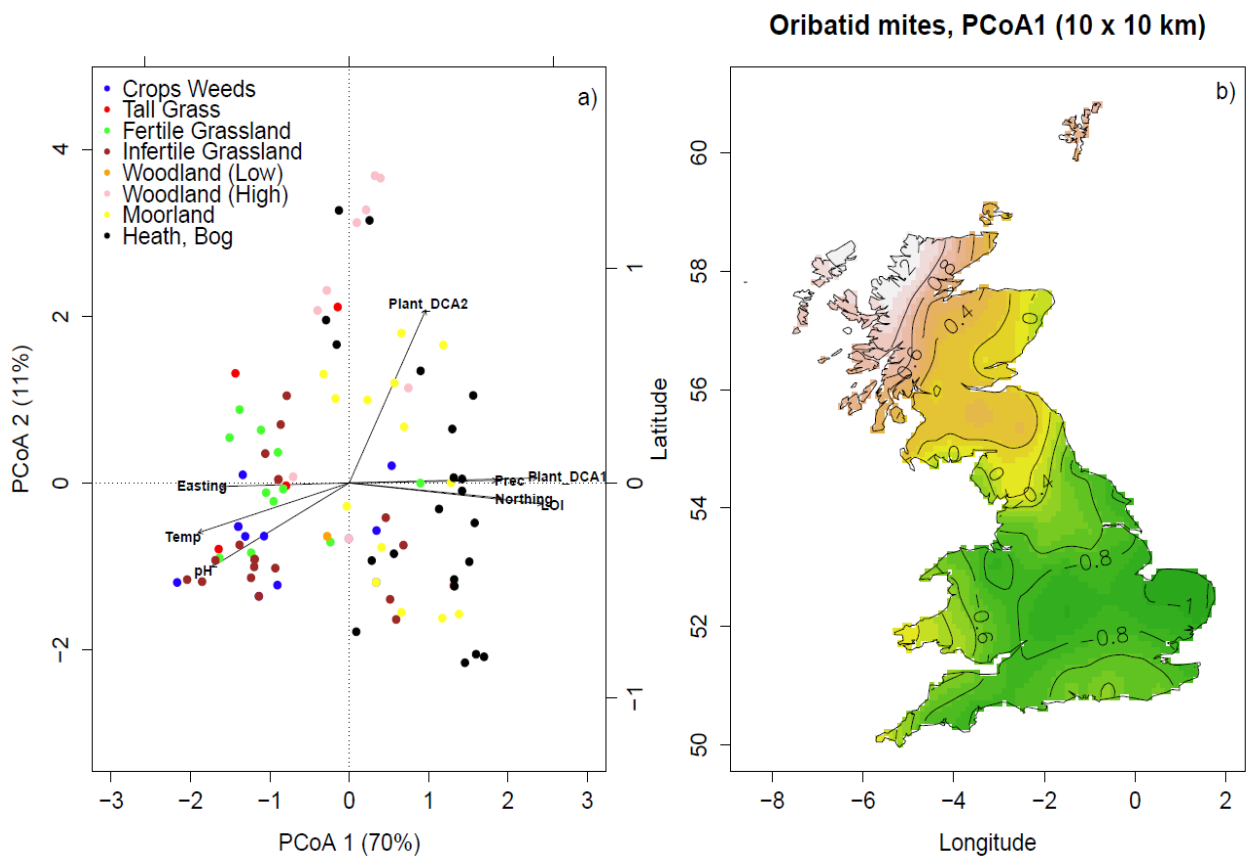


Figure 4

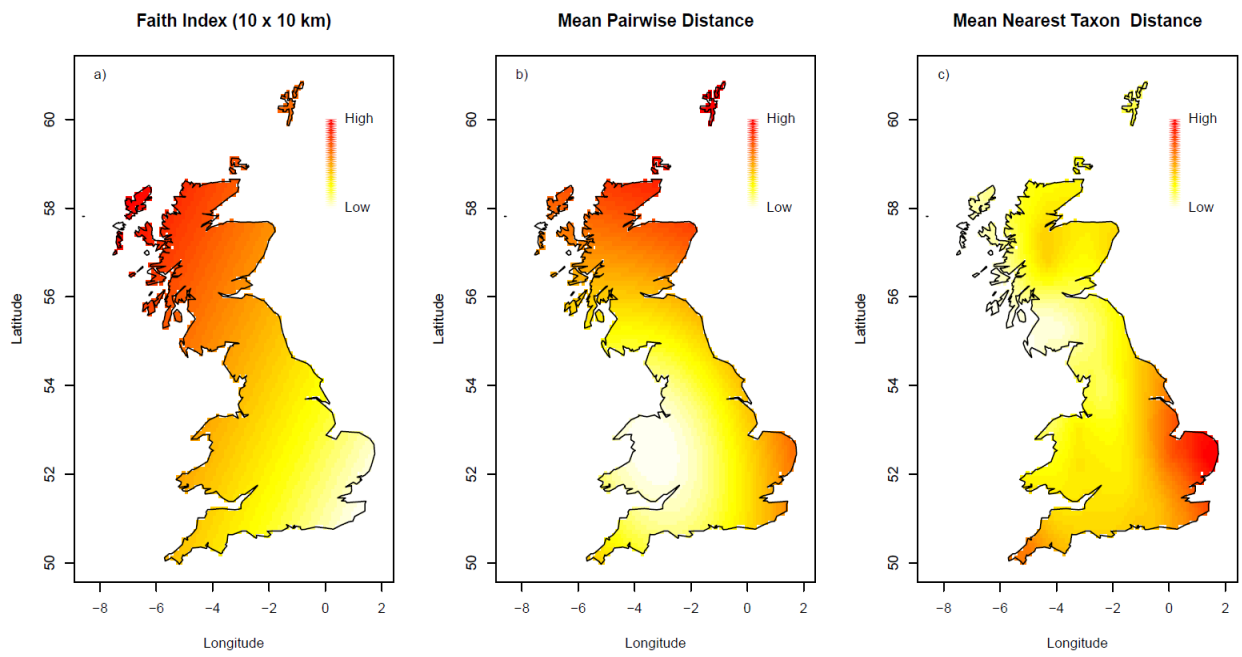


Figure 5

